

STUDIES IN CAPPARACEAE XXVIII:
THE *QUADRELLA CYNOPHALLOPHORA* COMPLEX

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ABSTRACT

Quadrella (DC.) J. Presl (1825) is a West Indian and Mesoamerican, dehiscent-fruited genus (Capparaceae) of 25 species covered with complex, variously branched or fused trichomes, was recently resuscitated from the breakup of the New World *Capparis* L., s.l. Within *Quadrella*, the lepidote or peltate pubescent complex of *Q. cynophallophora* (L.) Hutchinson includes two closely related, taxonomically problematic species and subspecies groups: *Q. cynophallophora* of the West Indies (with outlier populations in Florida and the Yucatan Peninsula) and *Q. isthmensis* (Eichler) Hutchinson in Mesoamerica. The former includes *Quadrella cynophallophora* s.s., widespread from the Bahamas through Hispaniola to Trinidad; *Q. jamaicensis* (Jacq.) J. Presl, from southern Florida to Hispaniola; ***Quadrella quintanarooensis*** Iltis & Cornejo, sp. nov., a local endemic of Cozumel Island and adjoining northeastern Yucatan in Mexico; *Quadrella gonaievensis* (Helwig) Hutchinson, a rare species of Hispaniola; and ***Q. siliquosa*** (L.) Iltis & Cornejo comb. nov., a montane endemic of Jamaica. From the American Virgin Islands, we describe two juvenile forms, ***Quadrella cynophallophora* f. *linearifolia*** Iltis, f. nov., and another from Jamaica, transferred from *Capparis*, ***Quadrella jamaicensis* f. *longifolia*** (Sw.) Iltis, comb. nov. The second group of taxa consists of *Quadrella isthmensis* (Eichler) Hutchinson, which we divide into three subspecies: *Q. isthmensis* subsp. *isthmensis* of Costa Rica and coastal Panama, ***Q. isthmensis* subsp. *glabripetala*** Cornejo & Iltis, subsp. nov., of Panama's Cordillera Central, and ***Q. isthmensis* subsp. *mexicana*** Cornejo & Iltis, subsp. nov., disjunct to Mexico's Yucatán Peninsula. The following taxa are lectotypified: *Quadrella cynophallophora* (L.) Hutchinson, *Q. jamaicensis* (Jacq.) J. Presl, and *Q. isthmensis* subsp. *isthmensis* (Eichler) Hutchinson. Finally, *Quadrella siliquosa* (L.) Iltis & Cornejo and its synonym *Capparis torulosa* Sw. are both neotypified. Descriptions, keys to taxa, distribution maps and illustrations are provided.

KEY WORDS: Capparaceae, *Quadrella*, Mesoamerica, Mexico, West Indies, Florida

RESUMEN

Quadrella (DC.) J. Presl (1825) es un género (Capparaceae) de las Indias Occidentales y Mesoamérica, recientemente resucitado de *Capparis* L., s.l., que comprende 25 especies caracterizadas por presentar complejos tricomas peltados a estrellados y frutos dehiscentes. En *Quadrella*, el complejo lepidoto o peltado *Q. cynophallophora* (L.) Hutchinson está compuesto por dos grupos de especies y subspecies taxonómicamente problemáticas y cercanamente relacionadas entre sí: *Q. cynophallophora*, principalmente distribuida en las Indias occidentales (con poblaciones en Florida y la Península de Yucatán); y *Q. isthmensis* (Eichler) Hutchinson, en Mesoamérica. *Q. cynophallophora* comprende *Q. cynophallophora* s.s., ampliamente distribuida desde Bahamas, a través de La Española hasta Trinidad; *Q. jamaicensis* (Jacq.) J. Presl, distribuida desde el sur de Florida hasta La Española; ***Q. quintanarooensis*** Iltis & Cornejo, sp. nov., una endémica local, de la isla Cozumel y la porción costera adyacente en el noreste de la Península de Yucatán, en Méjico; *Q. gonaievensis* (Helwig) Hutchinson, una rara endémica de La Española; y ***Quadrella siliquosa*** (L.) Iltis & Cornejo, comb. nov., endémica de las montañas de Jamaica. Describimos dos formas juveniles, ***Quadrella cynophallophora* f. *linearifolia*** Iltis, f. nov., de las islas Vírgenes y, ***Quadrella jamaicensis* f. *longifolia*** (Sw.) Iltis, comb. nov. es transferida de *Capparis*. El segundo grupo, estrictamente Mesoamericano, está compuesto por las tres subspecies de *Q. isthmensis* (Eichler) Hutchinson: *Q. isthmensis* subsp. *isthmensis* distribuida en Costa Rica y la costa de Panamá, ***Q. isthmensis* subsp. *glabripetala*** Cornejo & Iltis, subsp. nov., endémica de la Cordillera Central, en Panamá, y ***Q. isthmensis* subsp. *mexicana*** Cornejo & Iltis, subsp. nov., disyunta a la Península de Yucatán, en Méjico. Las siguientes taxa son lectotipificadas: *Quadrella cynophallophora* (L.) Hutchinson, *Q. jamaicensis* (Jacq.) J. Presl, y *Q. isthmensis* subsp. *isthmensis* (Eichler) Hutchinson. Finalmente, *Quadrella siliquosa* (L.) Iltis & Cornejo y su sinónimo *Capparis torulosa* Sw. son neotipificadas. Se provee una clave de identificación, descripciones, mapas de distribución e ilustraciones.

The almost exclusively West Indian-Mesoamerican genus *Quadrella* (DC.) J. Presl (1825), emended herein, is one of only two stellate to lepidote or peltate pubescent New World genera of Capparaceae with dehiscent fruits. *Quadrella*, a genus of 25 species, is characterized by a valvate calyx with four sepals in a single series. These may be 1), either very small and triangular with an open calyx aestivation long before anthesis in *Quadrella* subg. *Breyniastrum* (DC.) Iltis and half of the species of *Quadrella* subg. *Intutis* (Raf.) Iltis,

(*Quadrella domingensis* [Sprengel ex DC.] Iltis & Cornejo, *Q. ferruginea* [L.] Iltis & Cornejo, and *Q. incana* [Kunth] Iltis & Cornejo); 2), or with a closed calyx aestivation, i.e., temporarily fused and closed over the petal buds until or nearly to anthesis in subg. *Quadrella* and in the remaining species of *Quadrella* subg. *Intutis* (*Q. angustifolia* [Kunth] Iltis & Cornejo, *Q. alaineana* Cornejo & Iltis & *Q. singularis* [R. Rankin] Iltis & Cornejo) [Iltis & Cornejo 2010]).

Our view of the systematics of the *Quadrella cynophallophora* (L.) Hutch. complex, a taxonomical and nomenclaturally difficult group, is to place heavy emphasis not only on morphology of leaves, flowers and fruits but also on the mostly allopatric geographic distribution of its taxa. Thus, our systematic viewpoint is the exact opposite of that of the first author's former major professor, the late Robert E. Woodson, who in his treatment of Capparaceae for the Flora of Panama (1948) lumped all four of the then recognized taxa into one, all-encompassing *Capparis cynophallophora* without any further discussion. We, on the other hand, recognize the morpho-geographic reality and split this complex into several allopatric species and subspecies (Fig. 1), based on either *Quadrella cynophallophora* or *Q. isthmensis*. An exception lies in the *Q. jamaicensis* J. Presl–*Q. cynophallophora* geographic overlap in Hispaniola, and rarely with a *Q. jamaicensis* plant seen in the Bahama Islands, both of which are recognized herein as separate species based on their characteristic leaf shapes.

TAXONOMIC TREATMENT

Quadrella (DC.) J. Presl in Berchtold & J. Presl, *Prir. Rostlin* 2:260. 1825. **BASEONYM:** *Capparis* sect. *Quadrella* DC., *Prodr.* 1: 251. 1824. *Capparis* subg. *Quadrella* (DC.) Eichler in Martius, *Fl. Bras.* 13(1):269. 1865. **TYPE:** *Quadrella jamaicensis* (Jacq.) J. Presl (= *Capparis jamaicensis* Jacq.), neotype designated by Iltis & Cornejo 2010.

KEY TO THE QUADRELLA CYNOPHALLOPHORA COMPLEX

1. Ovaries at anthesis 3–6.5 mm; sepals 5–10(–11) mm; receptacle in fruits (2–)3–5 (–6) mm wide; stamens 16 to 35 (–40); leaf blades mostly lustrous above, usually uniformly lepidote or peltate, green or brownish-green beneath; Florida, through the West Indies to Trinidad and Barbados, disjunct to Mexico's Yucatan Peninsula (Cozumel Island and Quintana Roo) _____ **1. *Cynophallophora* alliance** (five species)
2. Flowers large, with petals 8–17 mm and sepals (5–)7–11 mm; stamens with simple or few-branched stellate trichomes at filament bases; anthers (2–)3–4 mm; southern Florida, West Indies, and in Mexico from the northeastern Yucatan Peninsula.
3. Gynophores conspicuous, 10–50 mm in flowers, to 80 mm in fruits; filaments 20–50 mm; petals 10–17 mm; common, the West Indies and southern Florida.
4. Leaf blades 3–8(–10) × 1–4(–4.5) cm, elliptic to narrowly obovate or oblong, rarely lanceolate (linear-lanceolate [to 17 cm] in juvenile leaves or stump sprouts), stiffly coriaceous and revolute, lustrous above; petioles 1–2 cm; seeds 5–8 × 4–6 mm, packed into mostly barely torulose capsules; throughout the West Indies and southern Florida, in Jamaica mostly in coastal lowlands.
5. Leaf blades ± elliptic, mostly 5–10 × 2–6 cm, with the apex acuminate or acute, sometimes obtuse to rounded but then often apiculate and not emarginate; central and eastern West Indies (Bahamas and Hispaniola to Puerto Rico, Trinidad and Barbados, sympatric with the following in Hispaniola) _____ **1. *Quadrella cynophallophora*** (L.) Hutchinson
5. Leaf blades mostly oblong or oblong-elliptic, mostly 3–7(–9) × 1–3(–3.5) cm, with the apex usually emarginate (notched) to rounded; southern Florida, Cuba, coastal Jamaica, Cayman and Swan Islands, sympatric with preceding species in Hispaniola, rarely in the Bahamas _____ **2. *Quadrella jamaicensis*** (Jacq.) J. Presl
4. Leaf blades 7–15(–20) × 4–9 cm, ± broadly elliptic, ± chartaceous, rather opaque above, on petioles (1.5–)2–4 cm; seeds 7–15 × 6–9 mm, spaced out in strongly torulose capsules; highlands of Jamaica at 200–800 m _____ **3. *Quadrella siliquosa*** (L.) Iltis & Cornejo
3. Gynophores in flowers and fruits highly reduced, to 5 mm or less or lacking; filaments 6–15 mm; petals 8–9 mm; endemic to Mexico (Cozumel Island and Quintana Roo, northeastern Yucatan Peninsula) _____ **4. *Quadrella quintanarooensis*** Iltis & Cornejo
2. Flowers small, delicate, with petals 6–7 mm and sepals 5 mm; stamens with densely lepidote-radiate or lepidote-stellate (many-branched) trichomes at filament bases; anthers 1–2 mm; very rare, scattered eastern half of Hispaniola (Haiti and eastern-most Dominican Republic) _____ **5. *Quadrella goniaeensis*** (Helwig) Hutchinson

1. Ovaries at anthesis 6.5–10 mm; sepals (9–)10–18 mm; receptacle in fruits 5–10 mm wide; stamens ca. 30 to 60; leaf blades opaque above (except *Quadrella isthmensis* subsp. *mexicana*), silvery lepidote-peltate beneath, with scattered darker bronze hairs giving the lower surface a peppered appearance; Panama and Costa Rica, disjunct westward to the central Yucatan Peninsula (northern Guatemala and Belize), and north to the Caribbean coast of Mexico's Yucatan _____ **1. Isthmensis** alliance (one species and three subspecies)
6. Petals densely lepidote without, sepals tomentose within; eastern Mexico (northern Yucatan and Campeche) south into Guatemala and Belize, disjunct to Costa Rica and lowlands of Panama.
7. Flowers larger, with petals 12–18 × 7–10 mm, stamens 4–7 cm, and gynophores 4–8 cm; fruits to 60 cm, on gynophores 4–8 cm and pedicels (1.3–)2–4.5 cm; leaf blades dull above when dry; Costa Rica and lowlands of Panama _____ **6. Quadrella isthmensis** subsp. *isthmensis* (Eichler) Hutchinson
7. Flowers smaller, with petals 9–13 × 6–7.5 mm, stamens 2–4(–4.5) cm and gynophores 1–4.5 cm; fruits to 23 cm, on gynophores 2–4(–5.5) cm and pedicels 1–2 cm; leaf blades often lustrous above when dry; Mexico (northern and central Yucatan Peninsula) to adjacent Guatemala and Belize _____ **7. Quadrella isthmensis** subsp. *mexicana* Cornejo & Ittis
6. Petals completely glabrous without, sepals tomentulose within; very rare, crest of the Cordillera Central of western Panama _____ **8. Quadrella isthmensis** subsp. *glabripetala* Cornejo & Ittis

1a. *Quadrella cynophallophora* (L.) Hutchinson, Gen. Fl. Pl. 2:309. 1967. (**Figs. 1–3**). BASIONYM: *Capparis cynophallophora* L., Sp. Pl. ed. 1: 504. 1753. TYPE: JAMAICA?: Left hand specimen, "Capparis 2," Hortus Cliffortianus Hb. (LECTOTYPE, designated here, BM-628728).

Shrubs or trees to 5(–10) m tall, to 40 cm dbh, rusty-brown peltate-lepidote throughout, the branchlet tips and peduncles flattened. Leaves ± coriaceous, evergreen, dark-green, often lustrous and glabrous above, densely covered with light golden brown (sometimes with scattered darker, rusty-brown) peltate-lepidote hairs beneath, ± elliptic to obovate, rarely lanceolate, acuminate or acute to rounded, often apiculate, cuneate to widely rounded at base (excluding the linear [to 15 × 2 cm] juvenile or stump sprout leaves), (3–)5–10 × 1.5–4.6 cm, the midrib sulcate above, the secondary nerves inconspicuous; petioles 0.5–2(–3.5) cm, canaliculate. Inflorescences terminal in leaf axils at ends of branches, subcorymbose, 1- to 7-flowered, the linear bracts ca. 2 mm, soon caducous; peduncles and stout 7–40 mm pedicels flattened, rusty-brown, densely lepidote; flower buds ovoid to lanceolate, pointed, longitudinally ± 4-ribbed; sepals at anthesis reflexed, ovate to lanceolate, 5–11 × 3–6 mm, densely rusty lepidote without, tomentose to tomentulose within; nectar scales flat, 1–2(–3.5) mm; petals divergent at anthesis, creamy white, soon fading (as do the stamens) to a pink or dark purplish violet, elliptic-obovate, about as long as the sepals, usually densely-lepidote without, glabrous within; stamens 20–35(–40), the filaments 2.5–5 cm, densely pilose with simple, usually white trichomes at the very base, the anthers 2–3.5 mm; gynophores 1.5–5 cm, glabrous, on androgynophores 1–1.5 mm; ovaries linear-cylindric, 3–7 mm, densely peltate-lepidote, the stigma truncate. Fruits linear-cylindric ± torulose siliquiform capsules, 4–40 × 0.4–1 cm, brown, densely lepidote, ± irregularly rupturing along (usually) one suture, the valves turning inside out to expose their bright orange to scarlet pulpy endocarp and the embedded bright orange to reddish arillate seeds, these often dangling from the replum by a thin funicular thread; gynophores (1–)1.6–8 cm, glabrous, clearly demarcated from fruit valves; receptacular disks in fruit, (2–)3–5(–6) mm diam.; pedicels 1.5–4 cm, lepidote; seeds (2–)5 to 40, oblongoid, 5–8[–10 mm in Hispaniola] × 4–6 mm, with a bright orange aril and thin testa, the embryo green throughout, much folded.

The lectotype of *Quadrella cynophallophora* was selected by Fawcett and Rendle (1914a: 142) with the statement that "*Capparis cynophallophora* L., Sp. Pl. 504 is based on the plant (sic!) *Capparis* 2 of *Hortus Cliffortianus* 204: Linnaeus merely repeats the diagnosis from the earlier work." However, unfortunately, *Capparis* 2 in the *Hortus Cliffortianus* Herbarium (Fig. 2) is a mixed collection, with the left hand specimen a branch of *Quadrella cynophallophora* labeled "*Capparis* 2" [and which we explicitly designate as the lectotype of that species], and the right hand branch clearly belonging to *Quadrella jamaicensis* (Jacq.) J. Presl (small, narrow, emarginate leaves, etc...), and simply another collection of that common coastal Jamaican species. No matter what Linnaeus (Anonymous 1933: 204) may say in *Hortus Cliffortianus* ("*Capparis*...foliis, ovalibus..."), he cites as his only reference Plukenet "Alm. 126. t. 172, f. 4" with "...foliis subrotundis..." from Barbados, this a drawing with typical *Q. cynophallophora* leaves.

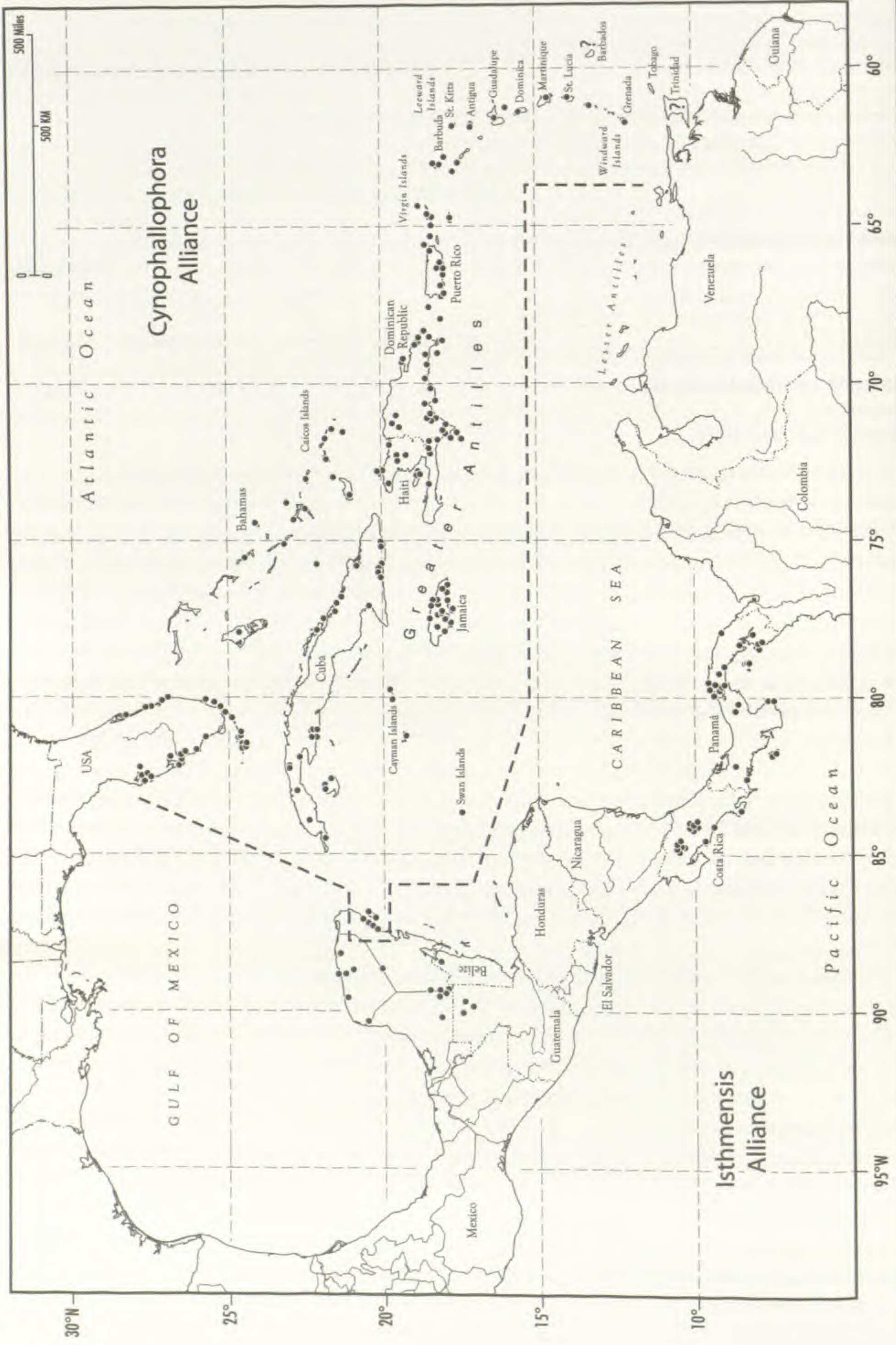


FIG. 1. Phylogeography of the *Quadrella cynophallophora* complex: The *Cynophallophora* group, ranging from southern Florida and the Bahamas through Jamaica and Hispaniola to Trinidad, and, disjunct, to Cozumel Island and adjoining mainland of the Yucatan Peninsula of Mexico; and the Mesoamerican *Quadrella isthmensis* group, ranging from Panama to Costa Rica and, disjunct, to the Yucatan Peninsula of Mexico, Guatemala and Belize.



FIG. 2. Hortus Cliffortianus Herbarium "Capparis 2" sheet (BM), a mixed collection with the left hand specimen the lectotype of *Quadrella cynophallophora*, and the right hand specimen a typical branch of *Quadrella jamaicensis*. Legend at bottom of left side, "p. 204 Capparis 2," refers to page 204 and the second *Capparis* listed in *Hortus Cliffortianus* (Anonymous 1937). Text in center reads "*Capparis jamaicensis* Jacq." on the top line and "*Capparis cynophallophora* L." on the bottom line.

Habitat and Distribution.—Central and eastern West Indies, from the Bahamas to Hispaniola (where it intergrades with *Quadrella jamaicensis*) and to the southern coast of Puerto Rico and through the Lesser Antilles to Trinidad and Barbados (Gooding et al. 1965), mostly in coastal, seasonally dry, evergreen woodlands, but also in a great variety of habitats, and often cultivated as hedges.

Phenology.—Flowering from April to January, fruiting throughout the year.

Vernacular names.—BARBADOS: Black Willow (E. Gooding 39, WIS); DOMINICAN REPUBLIC: Frijol (Valeur 403, WIS), Frijolillo (J. Schiffino 167, WIS), Olivo (J. Schiffino 27, WIS).

Selected specimens: **U.S. Virgin Islands:** St. Croix, Big fountain, A. Ricksecker (MU); St. Thomas, Water Bay, Eggers 417 (CAS); St. John, East End Quarter, P. Acevedo-Rodríguez et al. 1821 (WIS). **Puerto Rico:** El Tuque, near Ponce, H. Alain & P. Lioger 31206 (UPR); Salinas de Cabo-Rojo, P. Sintenis 578 (M); Mun. Manati, near Ciales, rte 632 near rte 149, C.M. Taylor et al. 7993 (NY); Mun. Guanica, Reserva Forestal Guanica, H. Iltis 30314 (WIS). **Dominican Republic:** Sierra de Neiba, Prov. Independencia, Cerros del Cao, T. Zanoni et al. 24814 (WIS); Peninsula de Barahona, Prov. Pedernales, 8 km sur del puerto de Cabo Rojo de Alcoa Expl. Co., T. Zanoni & J. Pimentel 26357 (WIS). **Guadeloupe:** Grande Terre, L'Auter Bord distr., E of Le Moule, G. Proctor 19916 (WIS). **Antigua:** St. Paul, Shirley Heights, G. Webster 13598 (WIS). **St. Maartens:** near top of Sentry Hill, A. Stoffers 4526 (A). **Barbados:** Newton, Christ Church, E. Gooding 39 (WIS).

1b. *Quadrella cynophallophora* (L.) Hutchinson, f. *linearifolia* Iltis, f. nov. (Fig. 3, upper left). TYPE: U.S.A. VIRGIN ISLANDS: St. John, East End Quarter, Hansen Bay, 0–10 m, dry scrubby coastal environment along a rocky shore, P. Acevedo-Rodríguez, A. Reilly & M. Davis 1808 (HOLOTYPE: NY, NY photocopy at WIS).

A *Quadrella cynophallophora* forma juvenilibus cum lamina linearis.

Distribution.—This form is found across the range of *Quadrella cynophallophora*.

2a. *Quadrella jamaicensis* (Jacq.) J. Presl, Prir. Rostlin 2:261. 1825. (Figs. 2B, 5A). BASIONYM: *Capparis jamaicensis* Jacq., Enum. Syst. Pl.: 23. 1760. TYPE: JAMAICA: tab. 101 in Jacquin, 1763 (LECTOTYPE, designated by Al-Shehbaz 1988: 296).

Capparis emarginata A. Rich. in Sagra, Hist. Fis. Cuba 10:28, tab. 9. 1845, syn. nov. TYPE: CUBA: Sagra (P) (lectotype designated by Al-Shehbaz in Flora of the Lesser Antilles-Dicotyledoneae 4(1):296. 1988).

Shrubs to small trees, peltate-lepidote throughout [except for the narrower, smaller leaves, very similar to *Quadrella cynophallophora*]. Leaf blades mostly oblong to oblong-elliptic, 3–9(–11) × 1–3.5 cm, with apex emarginate or notched to rounded, hard, shiny above, margin revolute; petioles 0.7–1.6 cm. Seeds 5–7 × 4–5 mm.

Habitat and Distribution.—This common coastal species is found in the United States in Florida (from Cape Cañaveral on the east coast and St. Petersburg Beach on the west coast, south to Key West), Cuba, coastal Jamaica, and the Cayman and Swan Islands, intergrading with *Quadrella cynophallophora* on Hispaniola, and rarely in the Bahamas.

Phenology.—Flowering from March to August, fruiting from June to October.

Vernacular names.—FLORIDA. Jamaica caper (D. Caldwell 8779, WIS), Black wattle, Black willow. CUBA. Carbonero, Ciguarayo, Mostaza, Mostacilla, P[enis] de perro (Roig & Mesa 1945), Moruro Prieto (Bro. León & T. Roig 11429, WIS).

Due to the ubiquitous confusion with the common *Quadrella cynophallophora* and the montane *Q. siliquosa* on Jamaica, we have chosen to cite only a few representative collections of *Q. jamaicensis* across its distributional range.

Selected specimens: **U.S.A. FLORIDA: Monroe Co.:** Florida Keys, Key West, A. Curtis 204 (BM, BKL, K, UT). **St. Lucie Co.:** ca. 2 mi S of hwy 712 on 707, S of Ft. Pierce, R. Wunderlin et al. 10153 (WIS). **Dade Co.:** Miami, Fairchild Trop. Garden, cult., H.H. Iltis 28580 (WIS). **Martin Co.:** E bank, St. Lucie River, E of Stuart, R. Kral 49263 (PH, VDB). **Lee Co.:** Sanibel Island, G. Cooley 2320 (USF); J.N. "Ding" Darling Nat. Wildlife Refuge, R. Wunderlin et al. 6278 (USF). **Pinellas Co.:** Madeline Key (Hospital Key), Fort De Soto Park, R. Thorne 33896 (IJ, RSA, USF, WIS). **Brevard Co.:** Malabar Cape, S of Melbourne beach, O. Lakela 28669 (DS, MEXU, USF, WIS). **Hillsborough Co.:** Cockroach Bay, Indian Shell Mound, S. Mortellaro 8 (USF). **Palm Beach/Martin Co.:** Jupiter Island, G. Cooley et al. 4875 (USF). **Sarasota Co.:** Sarasota, Longboat Key, O. Lakela & D. Laker 28686 (USF). **CUBA. Santa Clara:** Soledad State, Gavilán, J. Jack 5715 (WIS [MAD 16674]). Cienfuegos Bay, Punta Diablo, N. Britton & P. Wilson 5671 (NY). **Las Villas:** Vic. Soledad, A. González 594 (BM, FLAS, GH, IJ). **Isle of Pines:** Base of Sierra de Casas, Bro. Alain & E. Killip 2261 (GH, IJ). **Habana:** Near Batabanó, Bro. Alain 770 (IJ, US). **Pinar del Río:** Vic. Sumidero, J. Shafer 13516 (NY, PH, US). **Oriente:** Guantánamo Bay, U.S. Naval Station, woodlands, seaward point, N. Britton 2189 (NY). **Guantánamo:** Imias, R. Dechamps et al. s.n. (BR, 12335). **Without locality:** Wright 1870 (B, BM, GH, GOET, K, MO, NY, US, WIS fragm.). **CAIMAN ISLANDS. Caiman Brac:** betw. Hawksbill Bay & Goat Bay, S side, G. Proctor 29138 (IJ). **Grand Caiman:** near Sand Bluff, E end, M. Brunt 2002 (IJ). **Little Caiman:** 0.5 km W of Sparrowhawk hill, G. Proctor 35214 (IJ). **JAMAICA. Clarendon Parish:** Portland Ridge, A. Loveless 2272 (OFH). **St. Elizabeth Parish:** near Calabash Bay, R. Thorne & G. Proctor 48030 (NY, WIS). **Without Province:** Cane River Valley, W. Harris 9630 (BM, GH, K, MEXU, US). **SWAN ISLANDS.** Great Swan, G. Proctor 32521 (IJ). Little Swan, G. Clough 2 (IJ). **BAHAMAS. Long Island:** Clarence Town, S.R. Hill 2295 (VT).

2b. *Quadrella jamaicensis* (Jacq.) J. Presl, f. *longifolia* (Sw.) Iltis, comb. et stat. nov. (Fig. 4). BASIONYM: *Capparis longifolia* Sw. Prodr. (Swartz) 81. 1788. TYPE: JAMAICA: Swartz s.n. (HOLOTYPE: S! [WIS photo]; ISOTYPE: C! [IJ, WIS photo]).

This strikingly different form is evidently a stump-sprout or sterile, juvenile branch with narrow elongate leaf blades, common in this species and, in a homologous form, also in *Quadrella cynophallophora* f. *linearifolia* but apparently lacking in *Q. siliquosa*. *Quadrella jamaicensis* f. *longifolia* was illustrated by Plukenet (1696 tab. 327, fig. 6 p.p., the leafy branch only).

Distribution.—This form occurs across the range of *Quadrella jamaicensis*.

3. *Quadrella siliquosa* (L.) Iltis & Cornejo, comb. nov. (Figs. 5B, 6). BASIONYM: *Capparis siliquosa* L., Syst. Nat. ed. 10(2):1071. 1759. [pro parte]. *Pleuteron siliquosa* (L.) Raf., Sylva Tellur. 109. 1838. TYPE: JAMAICA: road to Troy, 18 Sep 1906, W. Harris 9488 (NEOTYPE, selected here: BM; ISOTYPES: A, GH, K, NY, US, WIS [fragm.]).

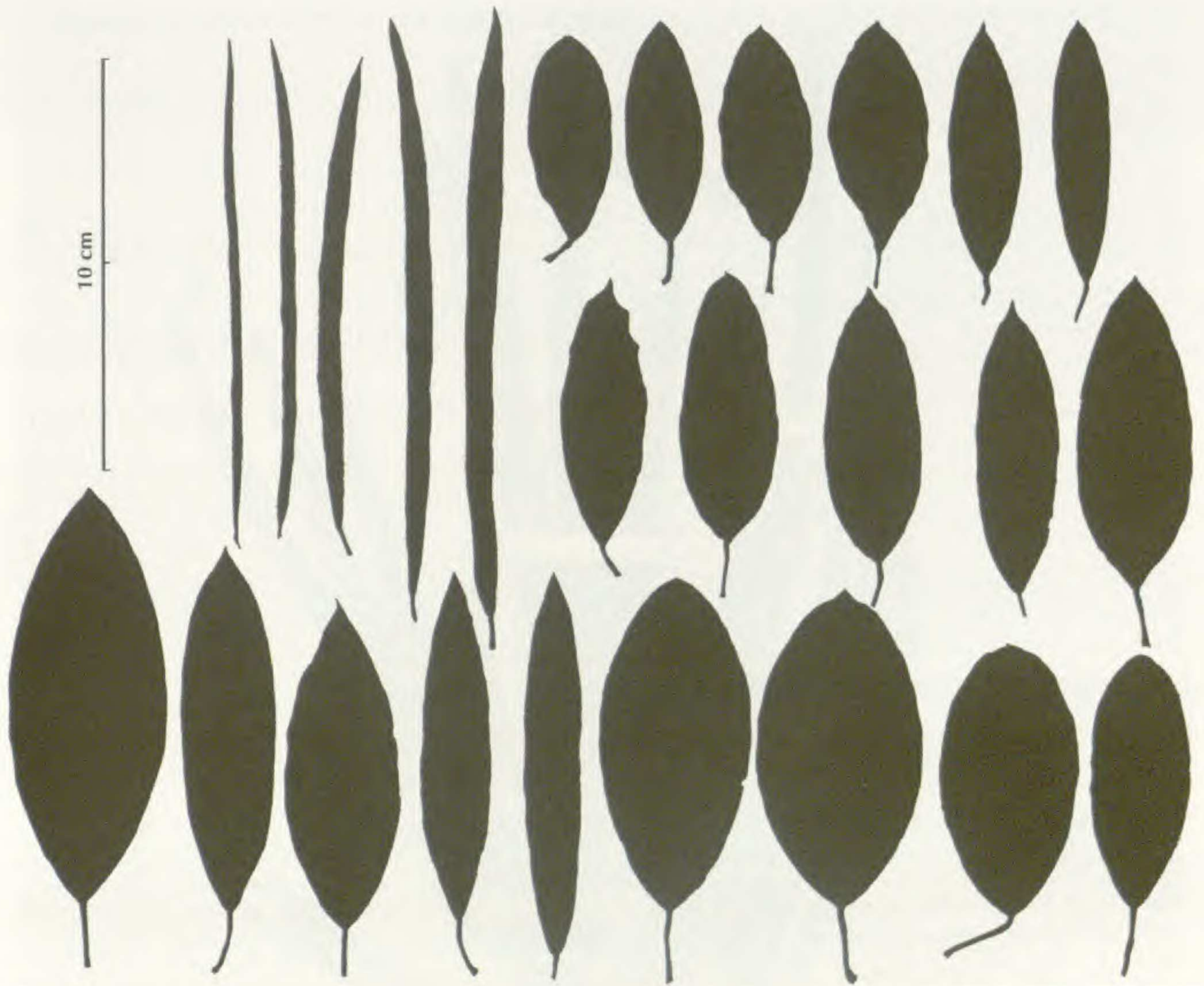


FIG. 3. Leaf blades shape variability in *Quadrella cynophallophora* on St. Maartens (of the former Dutch West Indies). Upper left: Stump sprout leaves, *Quadrella cynophallophora* f. *linearifolia* Iltis, all others, typical *Q. cynophallophora*, one leaf/collection (ex herb. Utrecht).

Capparis torulosa Sw., Prodr. 81. 1788. *Quadrella torulosa* (Sw.) J. Presl, Prir. Rostlin 2: 261. 1825. *Pleueteron torulosa* (Sw.) Raf., Sylva Tellur. 109. 1838. TYPE: Jamaica, s.d. (fr), C. Wright s.n. (NEOTYPE, designated here, S-05-9708, S photo at WIS).

Large shrubs or trees to 15 m tall, to 40 cm dbh, with dense bushy foliage. Leaves \pm broadly elliptic, acute to abruptly short acuminate to almost rounded to the tip, broadly cuneate to rounded at base, 7–15(–20) \times 4–9 cm, thinly coriaceous with mostly flat, occasionally revolute margins, glabrous above, peltate-lepidote beneath; petioles (1.5–)2–4 cm. [Juvenile leaves or stump sprouts not long and linear, as in both *Q. cynophallophora* and *Q. jamaicensis*]. Inflorescences small terminal corymbs or if lower, subterminal in the leaf axils; peduncles complanate-angulate, 3–6.5 cm, each bearing 3 to 7 flowers; pedicels 1–2 cm. Sepals lanceolate, 7–10 \times 5 mm, densely rusty lepidote without, tomentose within; nectar scales flat, one each projecting from the sepal inner base, ca. 1–2 mm; petals 9–13 \times 5–6 mm, divergent at anthesis, creamy white, densely lepidote outside, glabrous within; filaments ca. 3–5 cm, anthers ca. 3 mm; gynophores 2–5.5 cm, ovaries ca. 4 mm. Fruits distinctly torulose siliquiform capsules, (3.5–)10–36 \times ca. 1–1.2 cm, on gynophores (3.5–)5–8 cm; pedicels 1.2–2 cm; receptacles ca. 5 mm; seeds (1–)5–15(–20) or more per fruit, 7–15 \times 6–9 mm, separately spaced out, covered by a red aril embedded in red endocarp.

Both *Quadrella siliquosa* and *Q. torulosa* are based on the same polynomial, *Breynia* 2. *Arborescens, foliis ovatis utrinque acuminatis, siliqua torosa longissima* of P. Browne, Hist. Jam. 1756: 246, *pro parte* [excl. Plukenet, 1696: tab. 327, fig. 6; and in agreement with Eichler, 1865: 270 and Fawcett & Rendle 1914a:143,

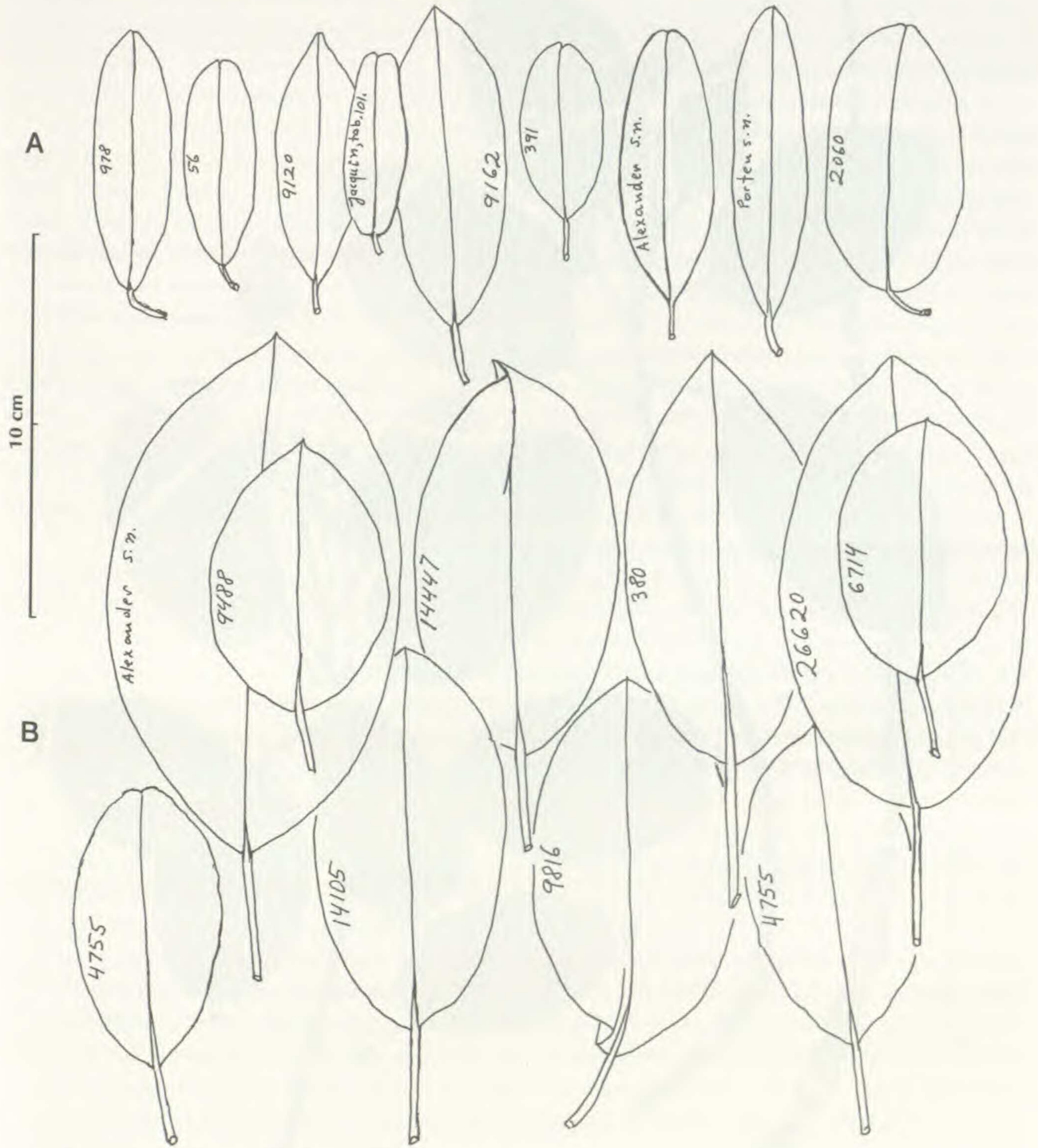


Jamaica: Swartz.

Capparis longifolia Sw. f.

FIG. 4. Holotype of *Quadrella jamaicensis* f. *longifolia* (Swartz s.n., 5): a juvenile form of the species, with linear oblong leaf blades.

Quadrella jamaicensis: Jamaica coastal



Quadrella siliquosa: Jamaica upland

FIG. 5. Leaf blades of *Quadrella* on Jamaica: A. the coastal *Q. jamaicensis*. B. the montane *Q. siliquosa*.

which is *Quadrella jamaicensis* f. *longifolia*, a linear lanceolate stump sprout or juvenile form of *Quadrella jamaicensis*]. For the lectotype of *Capparis siliquosa* L., Al-Shehbaz (1988: 296) selected "(1) siliquosa," Linnaean Herbarium sheet 664.8. Unfortunately, this sheet has two specimens attached to it, neither of which is *Q. siliquosa*. Since Linnaeus, in his original description of *C. siliquosa* (1759), cited Browne's (1756: 246, op. cit.) and then later (*Sp. Pl.* ed. 2, 1762; ed. 3, 1764) added "Planta forte" and also its resemblance to the preceding *C. cynophallophora* and "Habitat in Jamaica" (all four of these items applicable only to *C. siliquosa*),

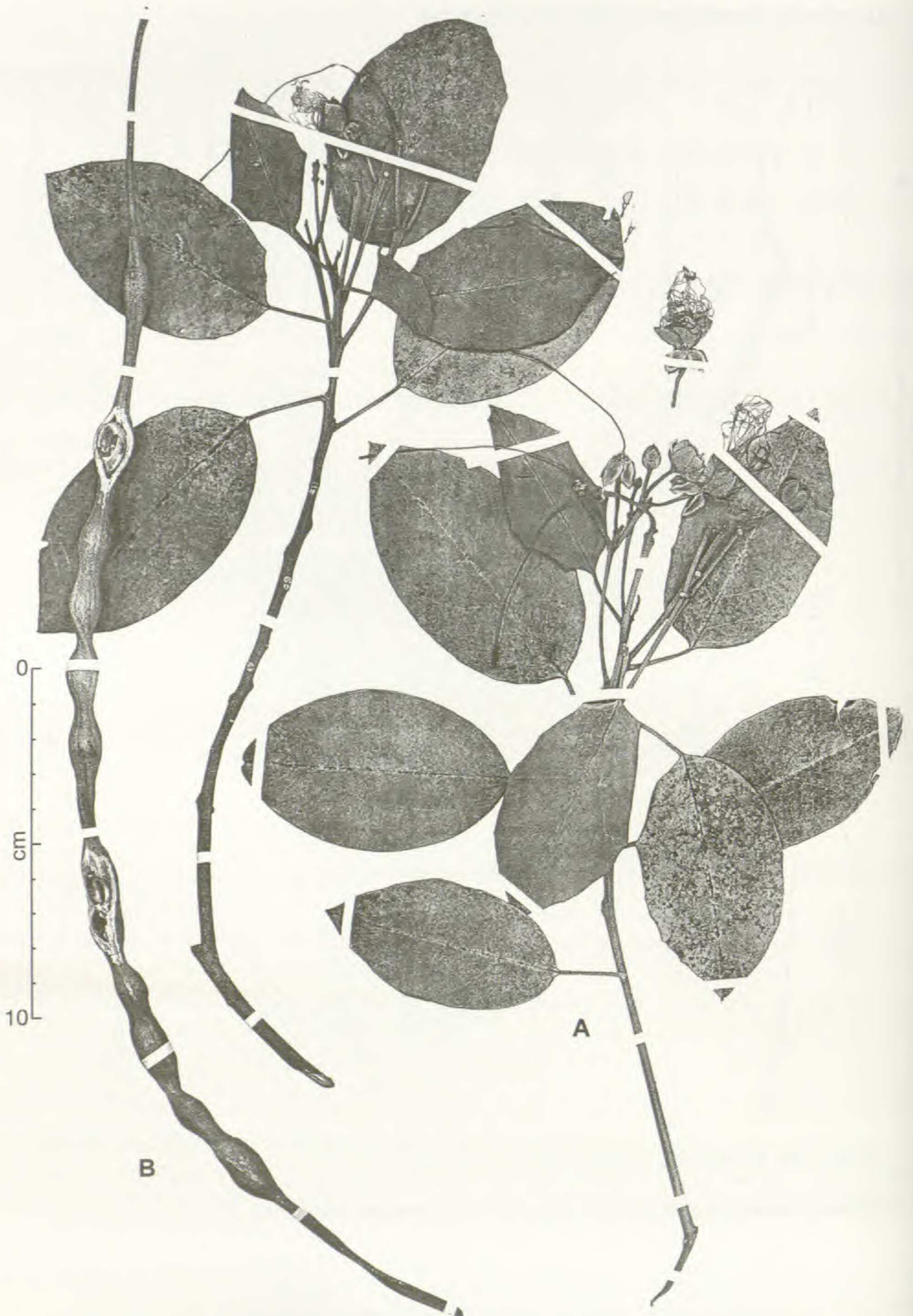


FIG. 6. Lectotype of *Quadrella siliquosa* (Harris 9488, BM), a Jamaican endemic: A. Flowering branch with 2–4 cm long petioles, 4–7 cm long gynophores and small ovaries. B. Mature silique.

we must reject Al-Shehbaz' choice of LINN-664.8. In this mixed collection, the right-hand specimen, labeled "(1) *siliquosa*," is a typical broadly elliptic, acuminate to acute-leaved *Q. cynophallophora* s.s. (relatively short-petioled, thus not to be confused with the longer petioled *Q. siliquosa*). The left-hand specimen, labeled "2. *cynophallophora*," is a typical *Q. jamaicensis* with emarginate, notched leaves. We have therefore chosen as a neotype Harris 9488, cited above (Fig. 6), about which there can be no argument as to its identity.

One of the pleasurable surprises of this revision was the rediscovery of the taxon now named *Quadrella siliquosa* (L.) Iltis & Cornejo (encompassing *Capparis torulosa* Sw., its ancient synonym). This is a broadly elliptic-leaved mesophytic tree, endemic to the montane woodlands and savannas of Jamaica, apparently closely related to *Quadrella cynophallophora* s.s. All the lowland, mostly coastal, plants in Jamaica belong to *Q. jamaicensis*, a shrub or small tree with uniformly small, hard, shiny, oblong to oblong-elliptic, most often emarginate leaves (Figs. 2, 5A), widespread from Florida to Cuba and occasionally Hispaniola, where it overlaps and intergrades with the more easterly *Q. cynophallophora*. The name *Quadrella siliquosa* must now be restricted to the large shrubs to trees of the Jamaican uplands, with much larger and thinner, more broadly elliptic leaves and almost rounded to broadly acute or abruptly short acuminate apices (Figs. 5B, 6), leaf size and shape presumably all adaptations to the cooler, moister, and shadier conditions of their upland, woodland habitats, as are their longer (2–4 cm) petioles. Although some specimens from the eastern range of *Q. cynophallophora* may have broad leaves, these tend to be more ovate or obovate-elliptic and are borne on shorter petioles (Figs. 2, 3), while those of *Q. siliquosa* are always symmetrically elliptic (Figs. 5B, 6).

The rediscovery of the name *siliquosa* was slow in coming. A review of many photocopies and a few old specimens of these upland plants in the Wisconsin Herbarium pointed to their frequent identification with the name *Capparis torulosa* by botanists of the early nineteenth century. This name, in turn, alerted us to the rather infrequent, strongly torulose siliquiform capsules with more distantly spaced seeds, which, in turn, separated from each other by conspicuous constrictions, helped explain Swartz's (1788) choice of his very apt epithet. Swartz's reference then led us to Browne's (1756) *Breynia* 2, a Jamaican tree different from the shrubby coastal *Breynia* 1 (= *Q. jamaicensis*), which in turn led us to the Linnaean *Capparis siliquosa*, also based on the same polynomial description. Swartz (1788: 81) and Browne (1756: 246) emphasized the very long ("longissima"), torulose ["torose"] fruits. Finally, DeCandolle's (1824: 252) statement "in fruticetis montosis Jamaicae..." clinched the identification of *Q. siliquosa* as the correct name, even though the immediate continuation of Candolle's sentence, "...et Barbados..." pointed to an easy misidentification with some of the broad-leaved and more lanceolate-elliptic collections of *Q. cynophallophora* from that most easterly island, where apparently that species is cultivated extensively.

For the past hundred and fifty years, however, all authors, from Grisebach (1864), Eichler (in Martius, 1865: 270 [both under *C. jamaicensis*]), Fawcett & Rendle (1914a: 143; 1914b: 231–232) to Al-Shehbaz (1988: 296) and Rankin & Greuter (2004), reduced both *Q. siliquosa* and *C. torulosa* to synonyms of *Q. cynophallophora* without further comment, even though on all bio-geo-ecological and morphological grounds the species are amply distinct. Only C.D. Adams, in his *Flowering Plants of Jamaica* (1972: 305–306), clearly notes both the ecological and morphological differences between *Quadrella jamaicensis* and *Q. siliquosa* (both under *C. cynophallophora* s.l., as applied to Jamaica).

Habitat and Distribution.—Jamaica, in upland woodland forests and often on limestone, from 500 to 2300 feet.

Phenology.—Flowering from (January) June to September, and fruiting from September to July.

Vernacular name.—JAMAICA: Zebra wood (Wright s.n., S).

In recent years, *Quadrella siliquosa* has rarely been collected and we are afraid, considering the human population explosion in Jamaica, and the dramatic local destruction of forests, that this interesting endemic species is slowly drifting into extinction. As handsome and bushy-leaved as that tree is reported to be, it surely deserves protection, if nothing else at least if need be by cultivation, or better still in a nature preserve.

Specimens examined: **JAMAICA. Parish not specified:** 1850, R. Alexander s.n. (K, WIS photocopy); 1857, Marsh 247 (K); 1858, Marsh 41 (K); Marsh 1528 (GOET, K); J. Hart s.n. (NY); Dr. Wright s.n. (K, S); Swartz s.n. (M); Lititz savanna, W. Harris 11780 (BM, CAS, GH, K, MO, NY, US); Bath, Wilson 380 (GH, K); between Ocho Rios & Roaring R., A. Prior s.n. (K); at Constant Spring, 1895, W. Harris 5718 (S

0510026), *E. Campbell* 5718 (BM, C, NY); Troy to Oxford, *N. Britton* 674 (NY, US, WIS); Postdam woodland, Santa Cruz, *W. Harris* 9816 (BM, C, K, NY, US); Robertsfield, *W. Harris* 7713 (A, BM, GH, K, US). **Manchester Parish:** Marshalls Pen, 2.25 mi NW Mandeville, *G. Proctor* 26620 (IJ, WIS [fragm.]); 1.6 mi NW of Rectory, Mile Gully, *L. Landrum* 4755 (WIS). **St. Elizabeth Parish:** between mileposts 4 & 5, Redgate to Ipswich road, *G. Proctor* 36828 (IJ); wooded limestone hill 1.5 mi N of shooters hill, *R. Howard & G. Proctor* 14105 (A, GH, IJ); Kaiser mine area S of Gutters, forested limestone hills near New buildings, *R. Howard & G. Proctor* 13846 (A, GH, IJ); Kaiser mine area at Comfort, on limestone hill, *R. Howard & G. Proctor* 14447 (A, BM, IJ). **St. Ann Parish:** Mason River district, ca. 3 mi NW Kellits P.O., *G. Proctor* 26473 (GH, IJ, NY, U); near road thru limestone hills betw. Cedar Valley & Ballintoy, *R. Anderson & D. Sternberg* 3070 (GH); Reynolds mine area near Lydford P.O., *R. Howard & G. Proctor* 14019 (A, GH, IJ, NY, US, WIS).

4. *Quadrella gonaievensis* (Helwig) Hutchinson, *Gen. Fl. Pl.* 2: 308. 1967. (**Fig. 8**). **BASIONYM:** *Capparis gonaievensis* Helwig, *Ark. Bot.* 22A:10. 1929. **TYPE:** HAITI: "Peninsula sept.-occidentalis ad viam inter Les Gonaïves et Hatte-Rocher prope mangrove communis," *E. Ekman* 8483 (HOLOTYPE: B!, B fragm. & photo at WIS; ISOTYPES: GH!, IJ!, US!).

Shrub or treelet to 7 m tall, abundantly branched, densely ferruginous-lepidote throughout. Leaf blades evergreen, chartaceous, dark green, usually minutely dark punctate, lustrous and glabrous above, lepidote beneath, elliptic to lanceolate, 3–7 × 1.2–3 cm, acuminate at apex, cuneate at base; petioles 1–1.5 cm; juvenile leaves linear to linear-lanceolate, 11–18 × 0.4 cm, with petioles 0.5–1.3 cm. Inflorescences corymbose; small delicate flowers on complanate peduncles 0.5–2.5 cm, and pedicels 0.6–1.2 cm. Petals broadly ovate, 6–7 × 5–6 mm, obtuse at apex, white; sepals ovate-elliptic, ca. 5 × 3 mm; nectar scales flat, one each projecting from inner sepal bases, ca. 1–1.5 mm; stamens 15 to 20, filaments 0.9–1.8 cm, densely lepidote-radiate or lepidote-stellate at base, the anthers 1–2 mm; gynophores 0.7–2 cm, ovaries oblong, ca. 3 mm. Fruits small siliquiform capsules, 2–6 × 0.4–0.5 cm, subtorulose, with red pulp, on short gynophores 8–16 mm; seeds 5–7 × 4–5 mm.

Habitat and Distribution.—A rare, highly localized but scattered endemic of Haiti and adjacent western parts of the Dominican Republic (Fig. 8), growing near mangrove communities and along rivers, characterized by its delicate small flowers with distinctive lepidote-radiate or lepidote-stellate trichomes at the base of the filaments. This species has usually been overlooked, or listed in synonymy under *Q. cynophallophora* (Urban 1920–21: 239; Al-Shehbaz 1988; Rankin & Greuter 2004).

Phenology.—Flowering from May to November; fruiting in April, September.

Specimens examined: **HAITI.** Gonaïves, Marchand, *W. Buch* 434 (B, IJ); ad Les Poteaux in collibus, *E. Ekman* 9059 (IJ, LL-TEX, WIS [fragm.], US); au Trou, *E. Ekman* 9882 (B, IJ); Iles Gonaïvensis, 1854 or 1855, *N. Prac* s.n. (P [2]). **SANTO DOMINGO. Barahona:** Am Yaqui Fluss, *Pater Fuertes* 111 (LD, P, U, US, WIS, Z). **Monte Cristi:** Valle del Cibao, betw. Navarrete & Villa Vasquez, *E. Ekman* 13120 (A, B, C, GH, LL-TEX, US). **Sine loc.:** 1853, *M. Schombourg* 25 (K, P).

5. *Quadrella quintanarooensis* Iltis & Cornejo, sp. nov. (**Figs. 7, 9A, B**). **TYPE:** MEXICO. QUINTANA ROO: Xcaret, a 5 km al S de Playa del Carmen, selva mediana, 15 Sep 1982 (fr), *E. Cabrera & H. de Cabrera* 3495 (HOLOTYPE: MEXU, MEXU fragm. at WIS; ISOTYPES: CAS, MO).

Species affinis *Quadrella cynophallophora* (L.) Hutchinson, a qua differt gynophoris extrematis minoribus vel absens, 0–5 mm longis, filamentis minoribus 6–15 mm longis, endemicus ex Isla de Cozumel et costa affinis ad Quintana Roo, Mexico.

Trees or shrubs 2–8 m tall, peltate-lepidote throughout. Leaf blades somewhat stiff, coriaceous, evergreen, narrowly elliptic, oblanceolate or obovate to broadly-elliptic or rarely ovate, 6–13 × (2.5–)3–6.5 cm, apex narrowly acute to long acuminate, at base cuneate to broadly truncate, with flat margins (when dry), usually lustrous above, densely covered beneath with colorless, peltate lepidote hairs with a light brown center, the wing several to many times slashed, sometimes the under-surface peppered with scattered darker orange hairs, secondary veins inconspicuous; petioles 0.7–2.3 cm, canaliculate. Flowers solitary or short axillary corymbose racemes at the ends of branchlets, the flattened peduncles 0.5–5 cm, bearing 1 to 6 flowers each; floral bracts soon caducous; flower buds spherical to ovate, longitudinally 4-ribbed, 6–9 mm; pedicels 0.5–2.2 cm. Calyx quadrangular, sepals ovate, 7–9 × 4–5 mm, reflexed at anthesis, yellowish tomentose within; nectar scales triangular, 1.5–2 × 2 mm, projecting from receptacle and the inner sepal bases; petals 8–9 × ca. 6 mm, stamens number unknown (ca. 30), with filaments 0.6–1.5 cm, and anthers 3–4 mm; androgynophores ca. 1 mm, the remarkably short, reduced gynophores only 0.5–5 mm or even absent; ovaries linear-cylindric, 4–6.5 mm, brown and densely peltate-lepidote, the stigmas truncate. Fruits

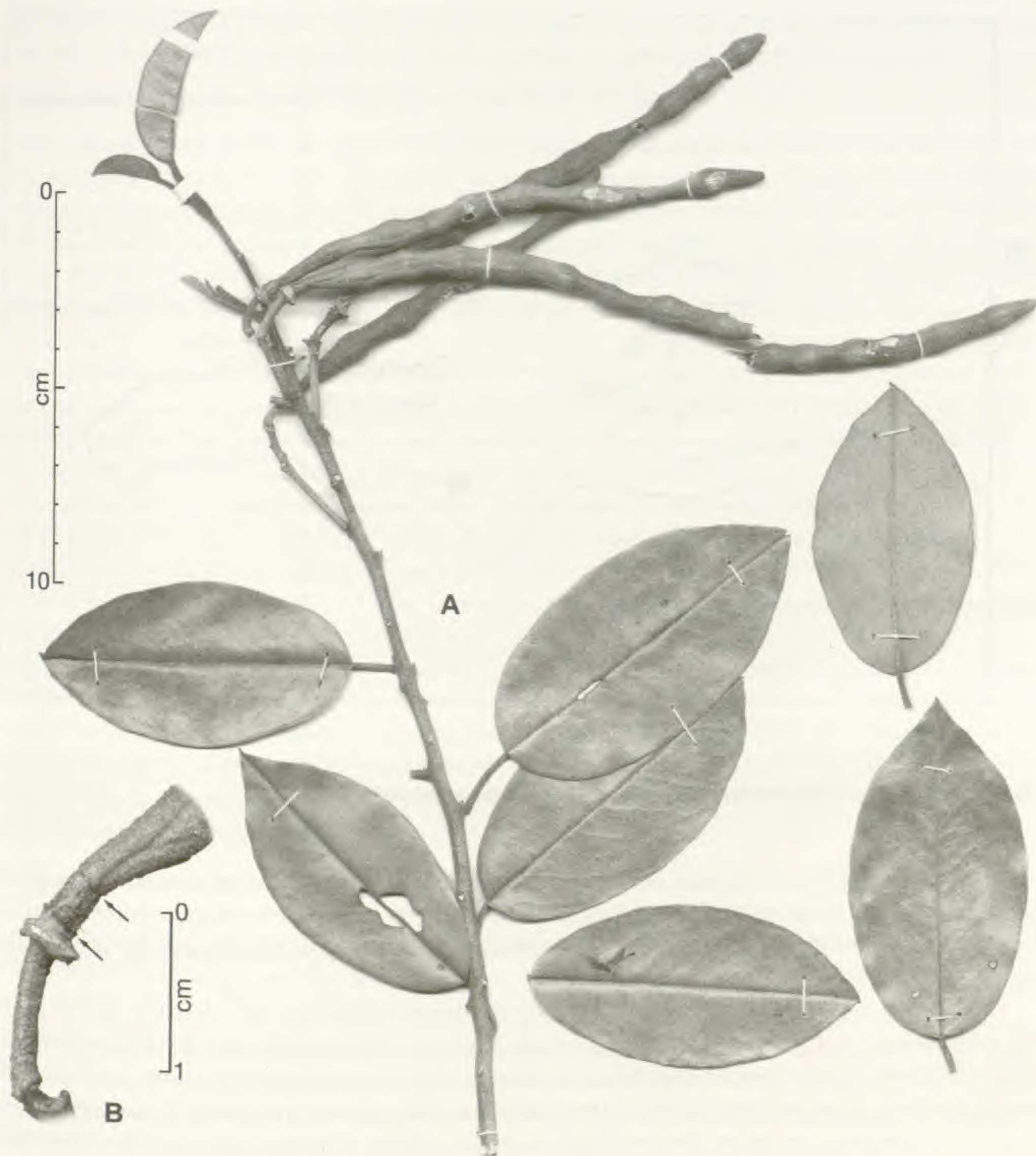


FIG. 7. Holotype of *Quadrella quintanarooensis* (Cabrera 3495, MEXU): A. Fruiting branch. B. Close-up of the characteristic, highly reduced gynophore in fruit.

linear-cylindric siliquiform capsules, 6–32 × 0.5–0.9 cm, brown, densely lepidote without, bright orange within, ± torulose, on very short and thick, 1–5 mm gynophores and 0.5–2.2 cm pedicels; seeds 5–8 × 4–6 mm, covered by an orange aril, the embryo green.

Despite the hundreds of thousands of tourists that now visit Cozumel Island and Tumul each year, it was not until the 1980s, when the tourist industry opened up the region, that Edgar Cabrera and associates (MEXU), discovered this interesting local endemic, which, apparently an offshoot of *C. cynophallophora* s.s. and generally so identified, differs from it by the highly reduced to essentially absent gynophores in flowers or fruits (Fig. 7B).



FIG. 8. Map of scattered geographic distribution of *Quadrella gonaievensis*, a rare endemic of Hispaniola.

In their variable size, acuminate outline, and the occasional peppered appearance of the peltate pubescence on their underside, the leaves of *Quadrella quintanarooensis* are similar to the northern collections of the nearby but allopatric *Q. isthmensis* subsp. *mexicana*, which may well be due to some past introgression that may have influenced its morphology.

By its very short or absent gynophore, this species resembles somewhat the distinctive, silvery peltate *Quadrella odoratissima* (Jacq.) Hutchinson (one of only three species of *Quadrella* sect. *Quadrella* not included in the *Q. cynophallophora* complex) distributed from southern Mexico to northern Colombia and Venezuela, the Dutch West Indies and Trinidad. However, *Quadrella quintanarooensis* differs from *Q. odoratissima* by its longer, quadrangular, not spherical calyx, longer rusty brown fruits, wider leaf blades with flat not revolute margins when dry, and light brown pubescence.

Habitat and Distribution.—In open, dry, highly seasonal tropical forests and woodlands (*selva baja mediana*, *selva mediana subperennifolia* [Rzedowski 1978]), often with *Pseudophoenix sargentii* H. Wendland ex Sargent (Palmae), *Manilkara* Adanson (Sapotaceae), *Coccoloba* P. Browne (Polygonaceae), *Beaucarnea* Lemaire (Agavaceae) and other xerophytes, on or near beaches at sea level to 50 m on Cozumel Island and the adjoining mainland of Quintana Roo, apparently not uncommon locally but restricted to this very small area on the northeastern coast of the Yucatán Peninsula of Mexico (Fig 9).

Phenology.—Flowering from April to July and fruiting from July through October.

PARATYPES: **MEXICO. Quintana Roo:** Mun. Benito Juárez, Puerto Morelos, Jardín Botánico CIQRO, H. Uitzil, M. Canche & S. Escalante 107 (MEXU [2]). Xcaret, 5 km S desviación a Playa del Carmen, E. Cabrera & H. de Cabrera 9267 (MEXU, MO); 5 km S Akumal, carr. Cancún-Tulum, E. Cabrera & H. de Cabrera 5530 (MEXU, MO); 6 km S Akumal, carr. Cancún-Tulum, E. Cabrera & H. de Cabrera 6501 (MEXU, MO); 8 km S Akumal, carr. Cancún-Tulum, E. Cabrera & H. de Cabrera 4739 (MEXU, MO); 10 km S Akumal, E. Cabrera & H. de Cabrera 3610 (MEXU, MO). Mun. Solidaridad, X'cacel-X'cacelito, ca. 13 km N Tulum carr. 307 Chetumal-Puerto-Juárez, C. Gallardo 2230 (MEXU); Isla Cozumel, 8 km S El Cedral, camino a Punta Celarain, E. Cabrera & H. de Cabrera 6741 (MEXU, MO). Mun. Cozumel,

1 km N Xel-ha, E. Cabrera & H. de Cabrera 7170 (MEXU, MO); 3 km N Xelha, O. Téllez, E. Cabrera & L. Rico 3570 (BM, MEXU, MO, NY); 12 km S de la ciudad de Cozumel, sobre la costera que va hacia la punta sur, E. Cabrera & H. de Cabrera 6361 (MEXU, MO).

6. *Quadrella isthmensis* (Eichler) Hutchinson, Gen. Fl. Pl. 2: 308. 1967.

Shrubs to slender trees 3–10 m tall, rusty brown peltate-lepidote throughout, the branchlet tips and peduncles flattened. Leaves thinly coriaceous, ± evergreen, dark green and glabrous above, densely covered with light golden or silvery (often peppered, with golden or rusty brown) peltate-lepidote hairs beneath; leaf blades conduplicate when young, elliptic, oblong elliptic to oblanceolate, sometimes rather abruptly acuminate into a sharp drip tip apex, usually cuneate to widely rounded at base, (excluding the linear, juvenile or stump sprout leaves) (6–)8–21(–26) × (2–)4–8.5 cm, with strongly impressed midrib on upper surface, secondary nerves rather inconspicuous on both sides; petioles (0.5–)1–4 cm, canaliculate. Inflorescences leafy corymbs, with 1 to 5 peduncles 0.5–10 cm, borne leaf axils at branch apices, each corymb 1 to 7-(to 13) flowered, linear bracts 2–6 mm, usually soon caducous; pedicels stout, usually ± flattened, 0.5–4.5 cm, bright rusty brown, lepidote; sepals valvate, before anthesis totally enclosing petals to form an ovoid to lanceolate, pointed, ± longitudinally ribbed bud, sepals after anthesis reflexed, ovate to lanceolate, (9–)10–18 × 5–8 mm, densely rusty lepidote without, tomentose to tomentulose within; nectar scales triangulate to deltoid and flat, one each projecting from inner sepal bases; petals divergent at anthesis, creamy white, soon fading (as do the stamens) to a purplish violet, elliptic-obovate, (9–)10–20 × 6–10 mm, glabrous within; stamens ca. 30 to 60, 20–70 mm, densely white pilose at base, anthers 3–5 mm; gynophore (10–)15–80 mm, glabrous, on an androgynophore 1–2 mm, ovaries linear cylindrical, 6.5–10 mm, densely peltate-lepidote, stigma truncate. Fruits linear cylindrical capsules, (6–)10–60 × 0.4–1.2 cm, dark rusty brown lepidote throughout, ± torulose, ± irregularly rupturing along (usually one) suture, the valves turning out to expose their pulpy bright orange to scarlet inner wall and embedded in it the bright orange to red arillate seeds, these often dangling by a thin funicular thread; gynophores 15–80 mm, glabrous, clearly demarcated from the fruit valve, receptacular disks in fruits 5–10 mm diam.; pedicels 1.5–4 cm, lepidote; seeds (3 to) 6 to 40, oblong, 6–8 mm, with bright orange aril, the embryo oblong, green throughout.

6a. *Quadrella isthmensis* subsp. *isthmensis* (Eichler) Hutchinson, Gen. Fl. Pl. 2:308. 1967. (**Figs. 9C, 11**). **BASIONYM:** *Capparis isthmensis* Eichler in Martius, Fl. Bras. 13:269. 1865. **TYPE:** COSTA RICA: "Habitat ad Costa Rica et Veraguas Americae Centralis," without date, C. Hoffmann & Warszewicz 217 (LECTOTYPE, designated here B, B fragm. at M, WIS).

Capparis chiriquensis Woodson, Ann. Miss. Bot. Gard. 35:92, fig. 49. 1948. **TYPE:** PANAMA. CHIRIQUÍ: vic. Puerto Armuelles, 0–75 m, 28–31 Jul. 1940, R. Woodson & R. Schery 846 (HOLOTYPE: MO; ISOTYPES: GH, US, US photo at WIS).

Leaf blades (6–)8–21(–26) × (2.5–)4–8.5 cm, matte above (when dry), on petioles to 4 cm. Inflorescence peduncle to 10 cm; floral bracts linear, 3–6 mm, usually soon deciduous in very young buds; flower buds ovate (in Panama) to mostly lanceolate (in Costa Rica), often with sharply angled longitudinal sutures; sepals ascendent to reflexed; petals ovate to elliptic, 12–18 × 7–10 mm; stamens 4–7 cm, gynophores 4–8 cm; fruits often very long, 10 to 60 cm, light to copper-brown, with elongate gynophores 4–8 cm, and pedicels (1.3–)2–4.5 cm; seeds 7–10 × 4.5–7 mm.

The lectotype of *Capparis isthmensis* is designated here because in the protologue, Eichler only cited "Habitat ad Costa Rica et Veraguas Americae Centralis: C. Hoffmann et Warszewicz," but the number of collection was not specified.

Typical *Quadrella isthmensis* is characterized by the large, elliptic, acuminate leaves with drip tips and often relatively long capsules, as well as by a silvery, pronouncedly bronze peppered, peltate-lepidote pubescence, especially on the underside of the leaves. The ovaries and petals are longer than those of *Quadrella cynophallophora* or *Q. siliquosa*; and the gynophores in flower and fruit are longer than those of the other subspecies in *Quadrella isthmensis*.

Quadrella isthmensis subsp. *isthmensis* presents no special taxonomic problems, except for occasional plants from the arid southern beaches and islands off Panama's Pacific coast, which tend to have smaller, thicker leaves, this apparently a response to local aridity. While these plants resemble *Quadrella cynophal-*

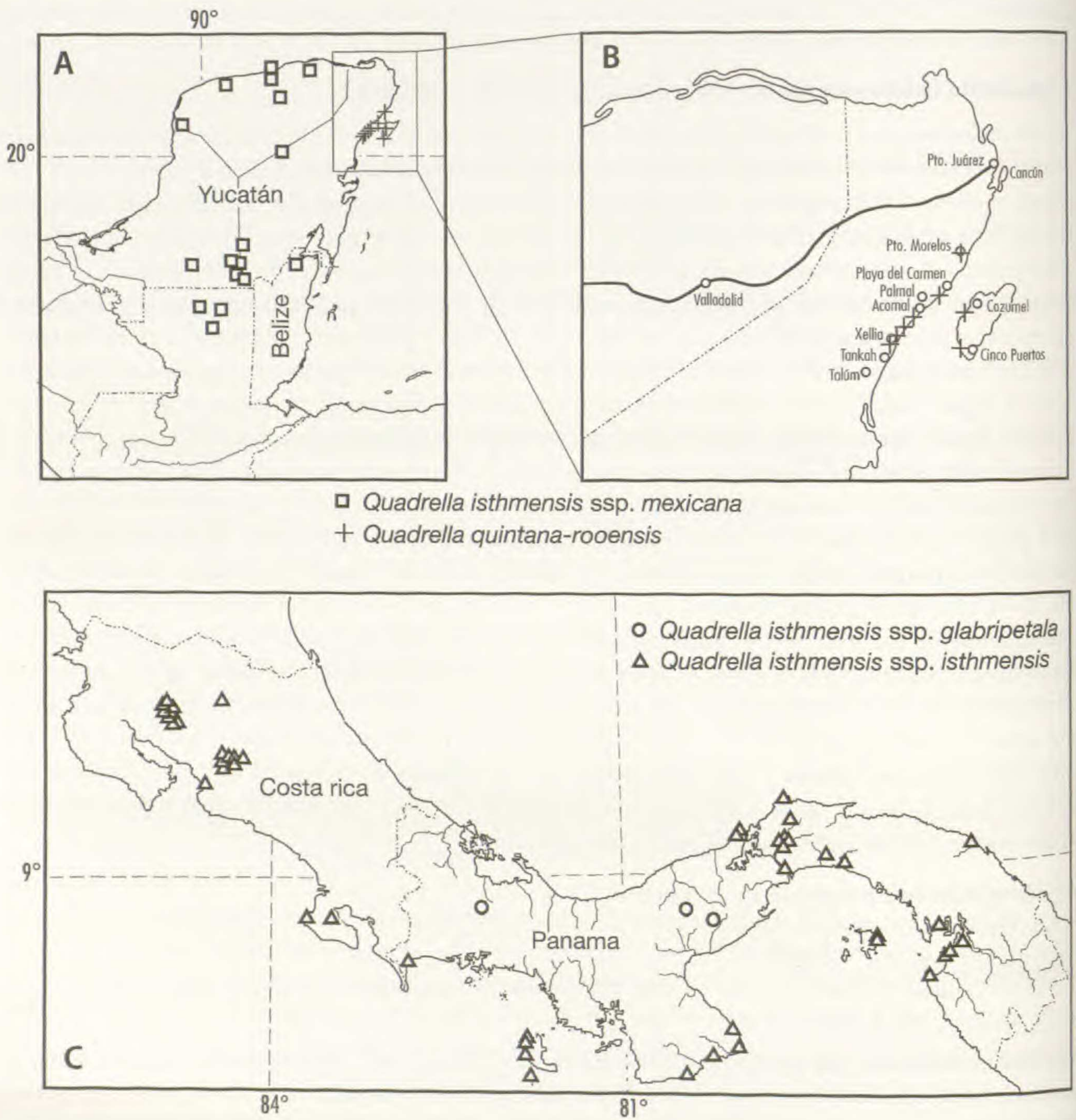


Fig. 9. Map of the members of the *Quadrella cynophallophora* complex on the Yucatan Peninsula of Mexico: A. *Q. isthmensis* subsp. *mexicana* (hollow squares) and *Q. quintanarooensis* (crosses). B. Map showing the localities on Cozumel Island and adjoining mainland in Quintana-Roo where *Q. quintanarooensis* (crosses) has been collected. C. Map of the distribution of *Quadrella isthmensis* subsp. *isthmensis* (hollow triangles) in Panama and Costa Rica, and *Quadrella isthmensis* subsp. *glabripetala* (hollow dots) in Panama only.

lophora, that species does not occur on the Meso- or South American mainland and is easy to tell apart by its narrower floral receptacle and the smaller ovaries, petals and leaves.

The seeds of *Quadrella isthmensis* are facultatively viviparous, sometimes even germinating within the fruit while yet borne on the plant (Castroviejo *et al.* 7186). This is an interesting observation considering the short seed viability, well known for a long time in two unrelated New World Capparid genera with green embryos linked to thin, flexible and slippery seedcoats (testas), namely, *Cynophalla* and *Quadrella* (subg. *Quadrella* and subg. *Breyniastrum*, but not in its subg. *Intutis*, with its hard, brittle testas linked to white or creamy embryos).

The first author may assume that their seed dispersing agents, be they bats, rats, birds or lizards (we

really do not know!), take a seed and, after swallowing the desired aril together with the thin testa (which, with a little manipulation easily slip off the distasteful acrid, now naked embryo), spits out the embryo, which then could start to photosynthesize and grow into a seedling soon after it hits the ground (Iltis, unpubl.).

A chance reading of the “*Capparis*” treatment in Linnaeus’ *Pflanzensystem* (1779), the rare 16-volume German translation from the Latin 13th edition of *Systema Naturae* (1764) (Anonymous 1933), has this to say about the seed germination of “*Capparis cynophallophora* L.” (by which the author meant not the densely peltate-pubescent *Quadrella cynophallophora*, but the glabrous *Cynophalla flexuosa* (L.) J. Presl (= *Capparis flexuosa* (L.) L.), [judging from its thick, stiff, smooth leaves with “glandulis axillaribus LINN. Syst. Veg. p. 405 Sp. pl. 721 [should be 722!], ...which on both surfaces are completely smooth...,” reflecting the horrible nomenclatorial confusion dating back to old Linnaeus himself between two of the most widespread and common Neotropical species that are also the two most common Capparids grown by the British and Dutch aristocrats, a confusion lasting well into the 20th Century (e.g., Pax and Hoffmann 1936:178):

“The fruits, as soon as they are ripe, split into two halves, which immediately twist back to let the white seeds, which are embedded in a soft scarlet pulp, fall out.... These seeds start to germinate almost immediately, and that is why one cannot send them to Europe [from overseas] any more than any of the other American capers, all of which quickly dry out and spoil.”

Habitat & Distribution.—This, the typical subspecies is found in Costa Rica, from sea level (in Corcovado National Park, Osa Peninsula) to 900 m (in the Cordillera de Tilarán, Río San Luis valley below Monteverde Cloud Forest Reserve), generally on the Pacific slope, in wet or moist tropical forests, and east to Panama, in drier habitats in the Pacific lowlands. In Panama, this subspecies is often found at or near sea level on beaches or behind mangroves, apparently not overlapping the range of the montane *Quadrella isthmensis* subsp. *glabripetala* in the Cordillera Central. Surprisingly, *Q. isthmensis* is not known to occur in Nicaragua even though, under the name of *Capparis cynophallophora*, it was optimistically listed as a species to be expected (Iltis 2001: 570).

Phenology.—Flowering from January through April (September to October), fruiting from June to December.

Vernacular name.—COSTA RICA. camarón blanco (white shrimp), (J. León 953, F; Zamora 1989).

Specimens examined. **COSTA RICA. Puntarenas:** forest near Palmar Norte, P. Allen 6639 (F); Res. Biol. Monteverde, Cordillera de Tilarán, J. Morales 2436 (INB, WIS); SW & below Res. Biol. del Bosque nuboso de Monteverde, H.H. Iltis et al. 30337, 30341 (WIS); Monteverde, 10 km SO, on road to Inter American hwy, W. Haber & W. Zuchowski 9933 (INB, MO, WIS); 9 km W Monteverde on road to Inter American hwy, W. Haber & W. Zuchowski 9248 (CAS, CR, INB [2], MO, VDB, WIS), W. Haber & W. Zuchowski 9761 (INB, MO, WIS); 4 km W of Monteverde, Cuencas del Lagarto y Guacimal, W. Haber & N. Obando 12128 (INB); trail from Playa Manuel Antonio to Puerto Escondido, M. Grayum & P. Sleeper 5921 (MO, WIS); Miramar, Cerro Zapotal, Quebrada Seca, L. Gómez, et al. 23994 (MO, WIS); Carara Reserve, M. Grayum & R. Warner 5707 (MO), sendero Quebrada Bonita a Bijagual, sitio Lomas Pizote, R. Zúñiga & Q. Jiménez 14 (MO, WIS); Cantón Golfito Jiménez, Río Piro y Quebrada Coyunda, A. Chacón 1039 (MO [2], WIS [2]); Alto Carbonera, cerro Osa, cabeceras de Quebrada Sombrero, G. Herrera 4344 (INB, MO, WIS); Osa, 3 km N de Playa Piro, Puerto Jiménez, Q. Jiménez et al. 659 (MO); Osa Peninsula, Corcovado Nat. Park, Sirena, R. Liesner 2976 (MO, WIS), P. Delprete 5152 (TEX), R. Liesner 2825 (MO); entre Senderos a Río Claro y a Los Patos, G. Fonseca 56 (INB, MO); R. Aguilar 2477 (CR, INB, WIS); O. Téllez 4247 (MEXU, MO); A. Chacón 86-05 (WIS); S. Knapp 2186 (MEXU, MO, WIS); W. Alverson 1837 (WIS); G. Maass 90 (INB, WIS); A. Gentry & OTS class 48484 (MO, WIS); C. Kernan 61 (MO); J. Saborio 83 (MO, WIS); G. Fonseca 14 (INB, MO); Res. For. Golfo Dulce, Rincón, L. Angulo 498 (INB). **San Jose:** Z. P. La Cangreja, Cerros de Puriscal, Santa Rosa de Puriscal, J. Morales & Q. Jiménez 3317 (INB, MO); Pérez Zeledon, Tinamaste, Finca de Los Suizos, A. Estrada et al. 1584 (MEXU); Río Naranja, versant Pacifique, A. Tonduz 7656 (BR, WIS fragm.). **Guanacaste:** Hojanca de Nicoya, J. León 953 (F); Zona Protectora Nosara, Res. For. Monte Alto, L. González & F. Hidalgo 2917 (INB); J. Morales 8711 (INB); Cerro San José, near H. Granadilla, C. Dodge & W. Thomas 6459 (F, MO); 5.4 mi. W of Tilaran on road to Laguna de Arenal, D. Stone 2168 (DUKE); J. Walker 405 (GH); vic. of Tilarán, P. Standley & J. Valerio 45705 (A); Zona Protectora Abangares, U. Chavarria & F. Alvarado 1732 (INB, MEXU). **Alajuela:** San Ramón, Finca San Gerardo, A. Carvajal 117 (MEXU, MO [2], WIS); near Atenas, in monte Aguacate, Ørsted 3168 (C); San Miguel de San Ramón, orillas del Río Barranca, A. Brenes 21952 (F, NY); San Pedro de San Ramón, A. Brenes 6686 (NY); Santiago, camino de San Francisco de San Ramón, A. Brenes 6668 (F, NY); Santiago de San Ramón, A. Brenes 6633 (F, NY). **PANAMA. Veraguas:** S shore of Ensenada Santa Cruz, N tip of Coiba Island, R. Foster 1621 (DUKE, F, MO, PMA), R. Foster 1644 (DUKE, F, MO, PMA); Isla Coiba, camp. Manila, S. Castroviejo & M. Velayos 8231 (MA, MO); Río Manila, B. Aráuz et al. 400 (MA, MO); Boca Grande, C. Galdames et al. 3653 (MA); Playa de la Salina, borde de la playa, S. Castroviejo et al. 7186 (MA, MEXU); Par. Nac. Coiba, Isla Jicarón, C. Galdames, et al. 4000 (BM, MA, MO). **Canal Zone:** Madden Dam, J. Ebinger 867 (F, PMA); Boy Scout Rd., Madden Dam area, D. Porter et al. 4054 (MO, WIS); J. Dwyer & Lallathin 8830 (F, MO); T. Elias 7509, 7510 (MO); Fort Clayton, 1 mi. bey. Madden Dam Bridge, M. Correa & R. Dressler 354 (DUKE, MO, PMA, SCZ); vic. Salamanca Hydro. Stat., Río Pequentí, R. Woodson et al. 1555 (A, MO, NA, NY, US); W of Limon Bay, Gatun Locks and

Gatun Lake, I. Johnston 1823 (A, MO, MEXU, NY); Victoria fill, near Miraflores Locks, P. Allen 1748 (MO, US); P. Allen 1760 (MO, NY, US); trail along Rio Petitpie, near road to Fort Sherman, S. Mori & J. Kallunki 5011 (MO, US, WIS [3]). **Los Santos:** Punta Mala, T. Croat 9757 (DUKE, MO, SCZ, WIS); E. Tyson 2727 (SCZ); Isla de Cañas, L. Carrasquilla 3011 (MO, PMA); playa de Cambutal, entre Punta Blanca y Punta Morro de Puercos, M. Correa et al. 4390 (PMA). **Comarca de San Blas:** Isla de Pinos, J. Kirkbride 208 (MO, NY, SCZ). **Darien:** vic. La Palma, H. Pittier 5504 (B, BM, GH, NY, US); Patiño, on cliff along beach, H. Pittier 6608 (GH, NY, US); J. Duke 10533 (MEXU, MO); Río Cucunati at Puente Quemado, J. Duke 8813 (MO). **Panama:** swamp betw. El Jagua Hunt. Club on Río Jagua & El Congor Hill, A. Hunter & P. Allen 480 (BM, BR, MO, WIS fragm.); near archeol. site at Madden Lake, A. Gentry 5015 (MO, NY, WIS); Chiltepe, L. Holdridge 6463 (DUKE, PMA), L. Holdridge 6465 (PMA, WIS); Isla del Espiritu Santo, J. Duke 10459 (MO); Perlas Islands, E. Tyson 5569 (DUKE, MO, SCZ); near Punta Garachine, J. Duke 10486 (WIS). **Colon:** along coastline betw. Garotte and La Guaira, D'Arcy 9367 (MO).

Subspecies of *Quadrella isthmensis* on Yucatan

The disjunct occurrence of *Quadrella isthmensis* subsp. *mexicana* on the Yucatan Peninsula is problematic, both in its geography, morphology, and relationships. Ranging from tropical seasonally dry, high forests in Guatemala and Belize, where very rare, all the way to the dry forests beaches and edges of mangroves far to the north in Mexico, the plants follow somewhat of a cline, from rather typical but, somewhat smaller leaves from around Lago Peten Itza and elsewhere in Peten Province and in Belize, to smaller, stiffer, more narrowly lanceolate-elliptic leaves in the dry deciduous forests of northern Yucatan (Fig. 9A).

Mexican specimens of *Quadrella isthmensis* subsp. *mexicana* were initially identified as *Capparis cynophallophora*, the leaves of which resemble somewhat the leaves of our Mexican subspecies, were it not that the latter species shares at anthesis the larger ovaries with *Q. isthmensis* and the characteristic bronzed dotted, peppered pubescence on the underside of the leaves. In addition, the closest *Quadrella* populations in Mexico are those of the endemic *Q. quintanarooensis*, and are apparently vegetatively closest to *Q. cynophallophora*. Thus, since we are faced with an isolated, somewhat morphologically differentiated population ca. 1000 km disjunct to the east from the main population of *Quadrella isthmensis* in Costa Rica and Panama, we have decided to name it:

6b. *Quadrella isthmensis* subsp. *mexicana* Cornejo & Iltis, subsp. nov. (Figs. 9A, 10). TYPE: MÉXICO, YUCATÁN: Las Bocas de Silam [Dzilám], May 1916 (fl), G. Gaumer & sons 23344 (HOLOTYPE: MO; ISOTYPES: BM, F, K, NY, US).

Subspecies affinis *Quadrella isthmensis* subsp. *isthmensis* (Eichler) Hutchinson, a qua differt petiolis minoribus (ad 1.7[–2.3] cm longis), petalis (9–13 mm longis), stamina (2–4[–4.5] cm longis), gynophoris (1–4 cm longis) et fructis (ad 23 cm longis).

Leaf blades 6–15 × 1.5–6 cm, often lustrous above when dry, on petioles to 1.7(–2.3) cm. Inflorescence peduncle 0.7–5.5 cm, floral bracts linear, ca. 2 mm, soon deciduous; flower buds ovate, with softly angled longitudinal sutures; flowers with petals lanceolate to somewhat elliptic, 9–13 × 6–7.5 mm; stamens 2–4[–4.5] cm, gynophores 1–4 cm. Fruits relatively shorter than the typical subspecies, to 23 cm, on usually shorter gynophores, (1–)2–4(–5.5) cm, and pedicels 1–2 cm; seeds 6–8 × 4–5 mm.

Habitat & Distribution.—This new subspecies, one of the successional elements from the mangrove's landward borders in Yucatan (Lira et al. 368), ranges inland through selvas medianas subperennifolias south to high forests in Guatemala and adjoining Belize.

Phenology.—Flowering from (February) April through May, fruiting from (June) August through September.

Vernacular name.—MEXICO, YUCATÁN: caimito-che (Enríquez 544, MEXU).

IUCN.—Because of the numerous collections gathered in recent years, this new subspecies deserves a lower concern, LC.

PARATYPES: **MEXICO, Yucatan:** Progreso, km 10–16 carr. Sierra Papacal a Chuburná Puerto, G. Campos & P. Simá 2828 (CICY, MEXU); Chichankanab, G. Gaumer 1910 (B, BM, C, F, GH, MO, NY, US); Port Silam [Dzilám], G. Gaumer 657 (BM, C, F, GH, K, LE, MO, NY, US), G. Gaumer 1548 (F), G. Gaumer 15685 (F, MO, WIS); S de Dzilám de Bravo, R. Durán & J. Trejo 1626 (MEXU); 3 km S Río Lagartos, E. Cabrera & H. de Cabrera 4670 (MEXU, WIS); Cenotillo, O. Enríquez 544 (MEXU, US, WIS neg. M4-10 & fragm.); Holpechén, camino blanco entre Kancabchén y Chunchintok, C. Chan 4025 (MEXU). **Campeche:** vic. Xpujil, crossroads 153 km E of Escárcega on Escárcega-Chetumal hwy, J. Shepherd 74 (F, MEXU, MICH, XAL, WIS); Mun. Calakmul, 7 km SO Dos Naciones, E. Martínez, D. Alvarez & B. Sanders 30511-C (MEXU); camp. costa Maya, 6 km O Narciso Mendoza, E. Martínez & D. Alvarez 30808 (MEXU); Narciso Mendoza, zona urbana, D. Alvarez 680 (MEXU); 1.5 km NW Pioneros del Río, camino a Santa Rosa, E. Martínez, D. Alvarez & C. Galindo 30661 (MEXU); 40 km



FIG. 10. Paratype specimen of *Quadrella isthmensis* subsp. *mexicana* (Gaumer 657, WIS): A. Flowering branches. B. Close-up of a post-anthesal flower in immature fruit, showing a gynophore relatively shorter than in the typical subspecies.

N Núcleo arqueol. Calakmul, C. Gutiérrez 5336 (MEXU); camino Pomuch a Isla Jaina, Hecelchakán, R. Lira, J. Flores, E. Góngora & P. Galván 368 (MEXU). **GUATEMALA. Peten:** Lake Peten Itza, betw. San José & El Remate, E. Contreras 6982 (LL-TEX, MEXU, MO, US); bordering Lake Peten Itza, El Jobo, E. Contreras 5748 (LL-TEX, US, WIS), E. Contreras 5749 (LL-TEX); ca. 2 km from San José, C. Lundell & E. Contreras 20392 (LL-TEX, WIS); 2 mi. SW Carmelita on the Paso trail, F. Engler 42-274 (F); Uaxactún to San Clemente, Bartlett 12791 (CAS, US). **BELIZE. Corozal:** Cerros Maya Ruins, Lowry's Bright, C. Crane 559 (LL-TEX). **Sine loc.:** A. Castillo 10 (WIS [MAD])

6c. *Quadrella isthmensis* subsp. *glabripetala* Cornejo & Iltis, subsp. nov. (Figs. 9C, 12). TYPE: PANAMA. CHIRIQUI: near Fortuna Dam Camp, seasonally dry evergreen forest, 8°43'N 82°14'W, 1200 m, 26 Feb 1985 (II), R.J. Hampshire & C. Whitefoord 111 (HOLOTYPE: MO; ISOTYPES: BM, PMA, WIS).

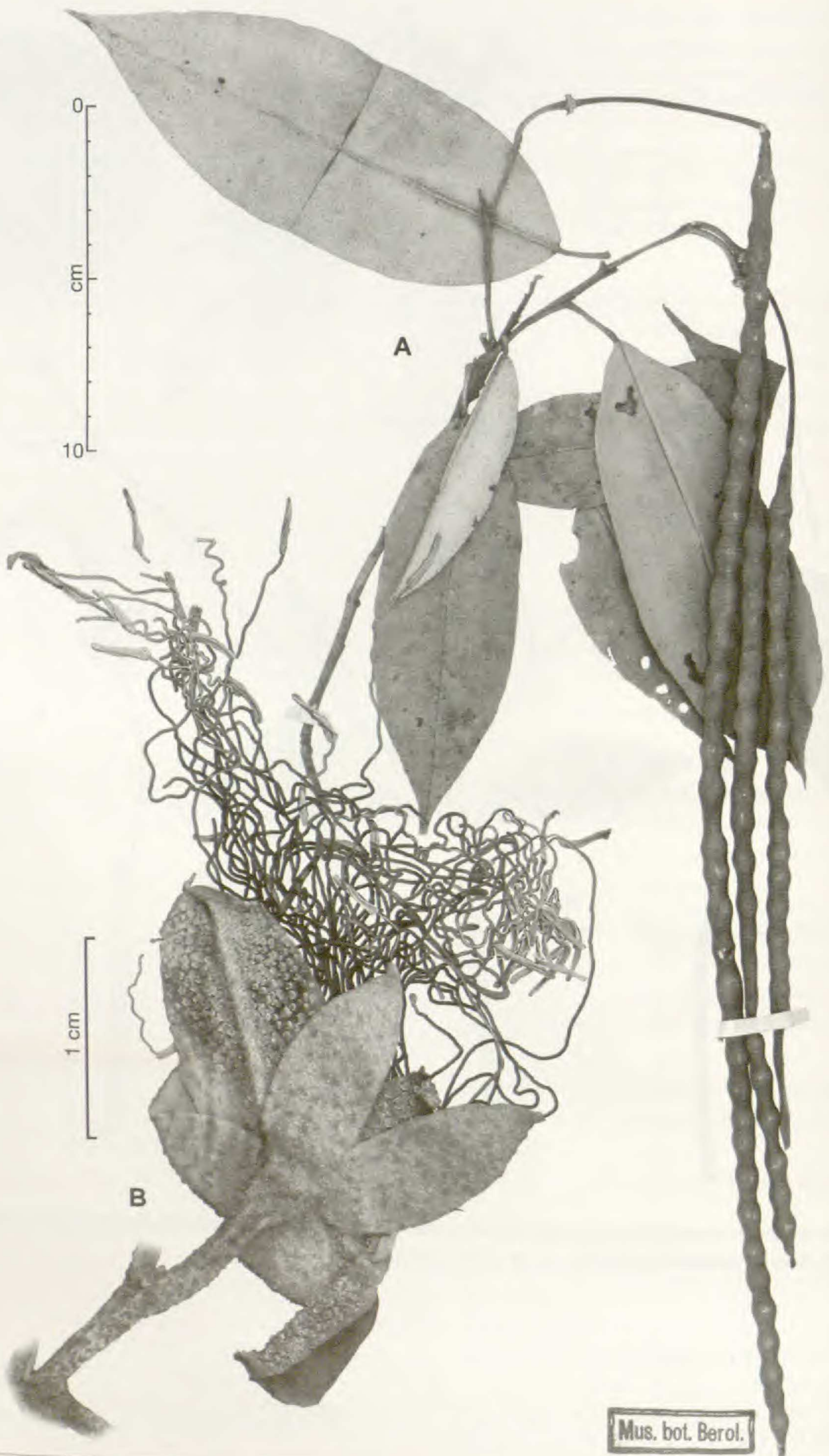


FIG. 11. *Quadrella isthmensis* subsp. *isthmensis*: A. Fruiting branch with long gynophores and torulose capsules. B. Close-up of a dried flower, showing the characteristic, abaxially densely lepidote petals (A: Hoffmann 755, B. B: Haber & Zuchowski 9761, WIS).



FIG. 12. Isotype of *Quadrella isthmensis* subsp. *glabripetala* (Hampshire & Whitefoord 111, WIS): A. Flowering and sterile branches. B. Close-up of dried, pre-anthesal flower with frontal sepal removed, exposing the characteristic, completely glabrous petals.

Subspecies affinis *Quadrella isthmensis* subsp. *isthmensis* (Eichler) Hutchinson, a qua differt petalis glaberrimis.

Leaf blades (5–)7–13 × (2–)3–4.5 cm, matte above when dry, on petioles 1.5–3 cm; inflorescences on peduncles 2–6 cm, bearing 1 to 2 flowers each; pedicels 3–4.2 cm; floral bracts linear, ca. 2.5 mm, soon deciduous. Sepals tomentulose adaxially, and petals glabrous abaxially; stamens ca. 30. Fruits not known.

Habitat and Distribution.—*Quadrella isthmensis* subsp. *glabripetala* is an apparently rare taxon, closely related to *Quadrella isthmensis* subsp. *isthmensis*, differing mainly by the strikingly obvious total absence of peltate hairs on the petals. That feature would seem to be trivial, were it not that the three known collections are widely spaced out for some 250 km along the crest of Panama's Cordillera Central, from the provinces of Coclé to Chiriquí, occurring at elevations from 500 to 1200 m, and are therefore also ecologically differentiated from the many other, and all coastal, Panamanian collections of *Quadrella isthmensis* subsp. *isthmensis* (Fig. 9C). This new subspecies is restricted to Panama and do not occur at higher elevations in Costa Rica.

According to one of the paratype collectors (Ken Sytsma, pers. comm.), *Quadrella isthmensis* subsp. *glabripetala* was collected at ca. 1400 ft. at the lower edges of dense, fairly wet, undisturbed cloud forests in one of the richest areas of endemism in Panama, a well known hot spot, thus now enriched by still another taxon.

Phenology.—Flowering from February through March.

PARATYPES: **PANAMA. Coclé:** Coclé, Cerro Pilón, hill below summit, above El Valle de Antón, 28 Mar 1969, J.D. Dwyer, L.H. Durkee, T.B. Croat, & J.R. Castillon 4545 (MO); above La Pintada, peak E Llano Grande-Toabré hwy, W. D'Arcy & K. Systma 14706 (MO, PMA, WIS).

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